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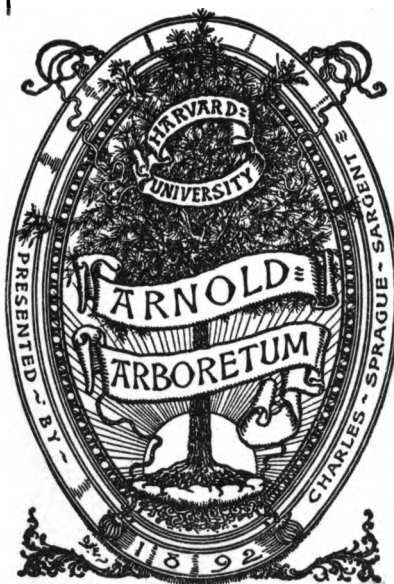
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[*Extracted from the LINNEAN SOCIETY'S JOURNAL—BOTANY,*
vol. xxii.]

ON THE
FLORAL CONFORMATION
OF THE
GENUS *CYPRIPEDIUM*.

BY
MAXWELL T. MASTERS, M.D., F.R.S., F.L.S., ETC.



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УНИВЕРСИТЕТ
ТРАДИЦИОН

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June, 1918
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On the Floral Conformation of the Genus *Cypripedium*.

By MAXWELL T. MASTERS, M.D., F.R.S., F.L.S., &c.

[Read 18th November, 1886.]

(PLATE XX. and ten Woodcuts.)

GENERAL CONFORMATION OF ORCHID FLOWERS.

The usual conformation of an Orchid flower*, the relative disposition of its parts, and the general course of their development are so well known that for the present purpose it is only necessary to advert to the relatively excessive development of the median petal or lip, and to allude to the construction of the "column" from three, or more frequently from six (potential) stamens arranged in two rows, an outer and an inner, and confluent with three styles.

According to the plan followed by Darwin†, and now generally adopted, the outer stamens are, for convenience' sake, denoted as A₁, A₂, A₃, the three inner ones being marked by corresponding smaller letters a₁, a₂, a₃. Similarly, the carpels of the gynæcium may be marked G₁, G₂, G₃. S may stand for the sepals, P for the petals, P₃ or L for the median petal or lip, and X for the staminode‡. In the great majority of Orchids the outer median stamen A₁, placed opposite the median petal, is the only one that attains its full development. Any or all of the other five may, under exceptional circumstances, be present, either in a perfect anther-bearing state, or more commonly in the guise of petals. Thus, in *Odontoglossum crispum* I have met with all six stamens fertile and free§. *Arundina pentandra* is described by Reichenbach as having five stamens; and Fritz Müller mentions

* See Eichler, 'Blüthen Diagramme' (1875), i. p. 179 *et seq.*; Gérard, "Sur l'homologie et le diagramme des Orchidées," Ann. Sc. Nat. Bot. 6^e sér. t. viii. p. 213, 1878; Van Tieghem, 'Traité de Botanique' (1884), p. 1387, and the same author, 'Sur l'Anatomie comparée de la Fleur' (1871), p. 140; Pfitzer's 'Morphologische Studien über die Orchideenblüthe' (1886) has been issued since this paper was written.

† 'Fertilization of Orchids,' ed. 2 (1877), p. 236.

‡ It must be borne in mind that throughout this paper the flower is supposed to be in the adult stage subsequent to any torsion, and that the numbers A₁ &c. do not apply to the order or period of development of the several parts.

§ Masters, 'Pflanzen Teratologie,' ed. Dammer (1886), p. 439, figs. 213, 214. In this edition numerous instances are cited of polyandry in Orchids in addition to those mentioned in the original edition (1869), p. 382. See also Masters, "Orchids single and double," in 'Gardeners' Chronicle' (1885), May 5, p. 597.

an *Epidendrum* one form of which is constantly triandrous (Bot. Zeit. 1872, no. 10, p. 152). By some observers it is considered that traces of the undeveloped stamens of the outer, and perhaps also of the inner, row are to be seen in the shape of lateral outgrowths from the column, or, as in *Cypripedium*, in the form of lateral lobes of the staminode; but this opinion, as also the view that one or more stamens are incorporated with the lip, I believe, for reasons hereafter given, to be erroneous*.

In *Zygostates cornuta* (according to Pfitzer, l. c. p. 88), in addition to the ordinary median stamen A_1 , there are present A_2 , A_3 , and a_3 , in the form of sterile filaments. Lindley, however ('Vegetable Kingdom,' ed. 3 (1853), p. 183^b), referred the staminodes of this plant entirely to the inner series. In *The-lychiton*, Endlicher, Iconog. t. 29, there is a central stigma surrounded by a lobed cup bearing on one of its lobes an anther. Crüger† describes and figures an *Isorchilus* in which the flower is normally triandrous, but which often bears five anthers with a filament proceeding from the front of the column just beneath the stigmatic cavity. Van Tieghem‡, relying exclusively on the distribution of the vascular bundles, gives an account of the arrangement of the parts, in some measure at variance with the generally received opinions, but he concludes thus:—"l'androcée des Orchidées est donc constituée idéalement par six étamines superposées, en deux verticilles ternaires aux divisions du perianthe."

The ternary nature of the gynæcium is generally admitted, though it is marked by abortion and concrescence. In a flower of *Pleione birmannica* recently examined all three stigmas were present. The distribution of the nerves in the column showed that the large wings of the column, which might readily be mistaken for lateral stamens A_2 , A_3 , were really subdivisions of A_1 .

The appended scheme, showing the relative position of the

Bract.		
	S_1	
P_1		P_2
	A_1	
a_1		a_2
	G_1	
G_2		G_3
	a_3	
A_2		A_3
	P_3	
S_2		S_3
Axis.		

Diagrammatic illustration of the arrangements of the parts of an Orchid flower.

* See Robert Brown, "Observations on Apostasia," in Wallich, *Plantæ Asiaticæ*, i. p. 74, and *Miscellaneous Botanical Works*, ed. Bennett (1866), i. 499.

† Journ. Linn. Soc., Bot. viii. p. 135.

‡ 'Anatomie Comparée de la Fleur,' p. 142.

parts in the generality of Orchids, may be useful for comparison. Letters in italics indicate parts that are generally absent, but which are potentially, and sometimes actually, present.

CONFORMATION OF CYPRIPIEDIUM.

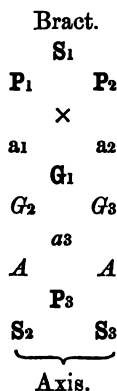
In an ordinary *Cypripedium* flower, as seen in the adult condition, there are three sepals, the median one free, the two lateral ones not only concrescent, so as to form in appearance a single sepal, but removed from their typical lateral position into a median one opposite to the median sepal. The result is that the flower appears to have a two-parted calyx, the significance of which will become apparent when the details to be hereafter given are considered. The corolla, or inner row of the perianth, consists of two lateral petals, and of one median labellum or lip, usually bag-shaped and differing greatly in appearance from the lateral petals.

The andrœcium is composed of one median stamen dilated into a broad shield-like staminode, and of two lateral fertile stamens within the preceding. The gynœcium consists of an inferior ovary, distinctly 3-celled in *Selenipedium*, but 1-celled with three parietal placentas in other *Cypripedia*. One of the three carpels is median, in the same line as the median staminode, the other two carpels being lateral and superposed to the lateral sepals. The styles are concrescent with the stamens into a column, the apparently solitary stigma being developed in the median line, superposed to the staminode.

Thus the largest sepal *S*₁, the largest petal *P*₃, the staminode *×*, and the stigma *G* are all in the median plane of the flower. This arrangement may be expressed by the accompanying plan.

The points specially worthy of note are the lip, the andrœcium, and the gynœcium. In the development of the flower, according to Crüger*, irregularity first shows itself in the median petal which develops itself into the lip.

As to the andrœcium, the generally accepted view is that which R. Brown originally propounded (but which he subsequently modified). According to this view the large staminode is the



Diagrammatic illustration of the arrangement of the parts of the flower in *Cypripedium*.

* Journ. Linn. Soc. Bot. vol. viii. p. 134, t. 9.

median barren stamen of the outer row, A₁. The two lateral fertile stamens, a₁, a₂, belong to the inner row. All the other stamens are absent. It is possible, especially in cases of *Peloria* (see *post.*), that the lateral stamens of the outer row, A₂, A₃, may be sometimes represented in the lateral lobes of the staminode, although, from the distribution of the vessels, I do not think this is usually the case. This staminode, moreover, is often more or less three-angled, three-lobed, or two-lobed with a central knob or short projecting filament. Link, as cited by Eichler *, was of opinion that the fertile anthers originated from the division of one median stamen, the staminode being looked on as an enormously developed connective. But although the staminode often shows signs of bi-partition, the whole weight of evidence, whether from morphology, teratology, or anatomy, is against Link's view. The teratological evidence will be alluded to later on, and that furnished by the anatomy of the column may be deferred till the nature of the style is considered.

The large stigma of *Cypripedium* occupies, as previously stated, a median position, and this position gives rise to some perplexity on account of its appearing to be a single organ.

The readiest mode of explaining the existence of a single stigmatic lobe would evidently be to assume that the two lateral carpels, at least their stylar portions, were abortive. An examination of the arrangement of the vascular bundles of the peduncle and of the column supplies another and more correct explanation.

Bract.

G

G G

Diagrammatic illustration of the position of the stigmas in *Cypripedium*, which, however, are concrescent, not isolated.

DISTRIBUTION OF THE VASCULAR BUNDLES.

Tracing the nerves from the stalk of the flower upwards to the ovary, and thence into the column, the arrangement is seen to be the following:—In the peduncle there are six vascular bundles in one ring. Following these upwards, three are found to correspond to the dorsal sutures of the carpels and three to the ventral or placenta-bearing margins. Although at first in one ring, at the level of the emergence of the perianth-segments, they form two rings one within the other, and their arrangement may be diagrammatically represented as follows, N₁, N₂, N₃ occupying the same positions as those occupied by the sepals, outer

* 'Blüthen Diagramme,' p. 181.

stamens, and carpels, while n_1 , n_2 , n_3 are in a line with the three petals and with the three inner stamens.

In fact, the median nerve N_1 , after leaving the ovarian wall, divides radially into two divisions, one of which passes into the median sepal S_1 , where it soon breaks up laterally into numerous subdivisions, while the other passes into the staminode $A \times$.

N_1
 $n_1 \quad n_1$
 n_3
 $N_2 \quad N_3$
 Diagrammatic
 illustration of the
 nerves at the base
 of the flower.

The nerves N_2 , N_3 pass into the corresponding lateral sepals without dividing radially, so that the cords corresponding to the stamens A_2 , A_3 are, in this case, entirely wanting. The intermediate nerves n_1 , n_2 each divides radially, one division passing into a lateral petal, the other into a fertile stamen. The median nerve of this series, n_3 , passes into the lip, P_3 , where it speedily trifurcates by lateral subdivision, but does not divide radially; for, as the inner median stamen a_3 is not developed, there is no vascular cord required for it*. The three cords for the gynæcial row are numerically as complete above as they are below the perianth, the primary nerves N_1 , N_2 , N_3 supplying the three carpels G_1 , G_2 , G_3 .

A difficulty, as before remarked, arises as to the large and apparently single stigmatic lobe which is placed in the median line. It might readily be assumed that the two lateral styles were in this case absent, while the median one, G_1 , was alone present. But this inference does not accord with the position of the placentas, two of which are placed laterally and one in the median line superposed to the lip. The placentas of course alternate with the styles, the styles in fact being prolongations of the dorsal sutures, while the placentas correspond to the united margins of three carpels. An examination of the vascular bundles in the style above the emergence of the stamens shows the three bundles N_1 , N_2 , N_3 very distinctly alternating with the 3-lobed mass of conducting tissue continuous below with the placentas. Into the stigmatic lobe itself, which is a triangular cushion-shaped body with the apex of the triangle in the middle line, it has appeared to me that the median bundle, N_1 , does not always enter, though it does so in some cases. The other two bundles, N_2 , N_3 , corresponding to G_2 , G_3 , however, are always

* Darwin's view that the nerves corresponding to A_2 , A_3 are in any degree incorporated with the lip is, I believe, an error; the nerves figured by him at the side of the lip result merely from the lateral branching of the bundle n_3 .

present. The mass of the stigmatic lobe is made up of large thick-walled polygonal cells, many with nuclei and nucleoli; through this mass of parenchyma the vascular cords pass, the tracheæ being nearest to the lower or anterior edge. The lower or anterior part of the stigmatic lobe consists of several layers of cells of a very different character from those constituting the bulk of the lobe. They are elongated or club-shaped, in several layers, disposed more or less horizontally, thin-walled and nucleated, and bounded on the lower surface by a layer of papular cells.

This layer of stigmatic tissue, though to outward appearance unbroken, is seen, on inspection of microscopic sections, to pass inward and to separate the lobe into two divisions, corresponding to G₂ and G₃. Perhaps in some species G₁ may be cut off in a similar way, but this has not been the case in any of the flowers examined by me. The stigmatic lobe, therefore, so far from being single, as it appears to be at first sight, is certainly two-fold and, perhaps, in some species three-fold, the two or the three styles at their uppermost ends being united in the median line like the two lateral sepals. The column of *Cypripedium*, therefore, is made up of three stamens and of three styles. Of the three stamens the upper median belongs to the outer row and is developed as the staminode; the other two lateral ones are fertile and belong to the inner row. Of the three ovaries and three styles all remain, but of the three stigmas the upper or median one becomes abortive, while the two lateral ones are joined into one compound lobe*.

TERATOLOGY OF *CYPRIPEDIUM*.

Adverting now to the teratological appearances presented by this genus and its allies, I propose to confine attention to those malformations which more directly elucidate the plan of Orchid-structure, and to omit reference to those numerous cases of pure distortion or perversion which have no direct morphological significance from the present point of view.

So regarded, these malformations may conveniently be grouped under the heads of defect, of excess, or of perversion of the natural

* The description above given of the course of the vascular bundles of the column &c. agrees in the main with that given by Van Tieghem, 'Anatomie Comparée de la Fleur,' p. 144, tab. xii. figs. 209-219, and with that propounded by Gérard, *l. c.* p. 236. Van Tieghem, however, says nothing about the arrangement of the cords in the stigmatic lobe, nor is it alluded to by any other author, so far as I am aware.

process of development. Some of these changes may thus be considered as progressive, others as retrogressive, and not infrequently as reversions to a prior and simpler condition*.

OLIGOMERY.

I. *Reduction of Parts*.—A dimerous condition is one of the commonest deviations from the usual typical structure of Orchids in general. This arrangement may be thus represented, the two sepals being lateral, the solitary fertile stamen A and the stigma G being in the median line. This dimerous condition has some indirect analogy with the natural arrangement of parts in *Cypripedium*, where in the adult flower there are two sepals only (one of these, however, resulting from the concrescence of two), and in the presence in the median line of two much-modified parts, the lip and the staminode, the inner staminal whorl being represented by a pair of organs placed at right angles to these, and, as it were, decussating with them.

In abnormal flowers of *Cypripedium Sedeni* the dimerous condition is associated with the presence of a single median fertile stamen in the position usually occupied by the staminode X. In these cases the median sepal is generally absent, whilst the two lateral ones are either united or partially separated, and more or less dislocated or turned to the lower part of the flower. No lateral petals are formed, but a petal is placed above in the median line, in the position usually occupied by the median sepal, and in form and colour like one of the lateral petals. Opposite to this petal is placed a second one, lip-like in character, or sometimes flat†.

P
S A S
G
L

Diagrammatic
illustration of di-
merous Orchid.

Bract.
S
P P
X
a1 a2
G
L
S S
⏟
Axis.

Diagrammatic
illustration of ar-
rangement of parts
in *Cypripedium*.

* A very large number of specimens have been examined by myself during the last few years, and upon this examination these remarks are, for the most part, based. I avail myself, however, of this opportunity of thanking Mr. Hansen, of St. Alban's, for the privilege of inspecting a large number of drawings executed by him in the rich Orchid nursery of Mr. Sander.

† See Le Marchant Moore, in 'Journal of Botany' (1879), vol. xviii. p. 1; Masters, 'Vegetable Teratology,' p. 401; German edition, ed. Dammer (1886), p. 460; Magnus, Sitzungsbericht d. Gesellsch. Naturforsch. Freunde zu Berlin,

In a monandrous flower of *C. barbatum* sent me by Mr. Bull there were two lateral sepals turned downwards, an upper median

Fig. 1.

Fig. 2.

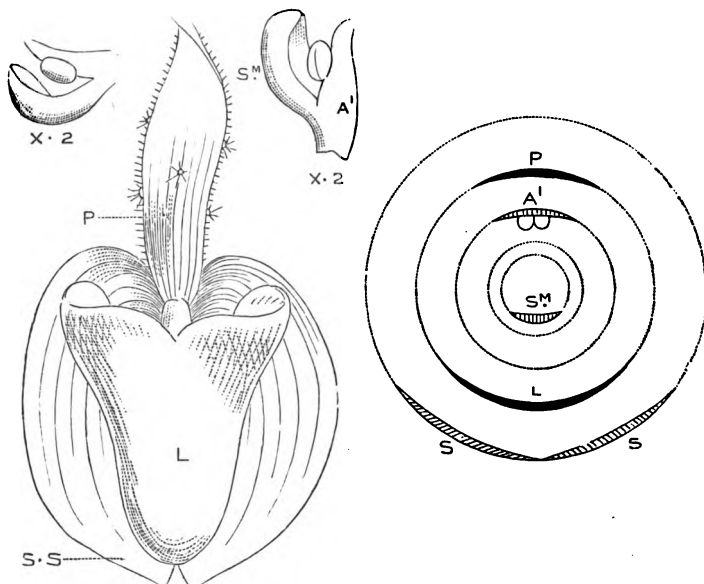
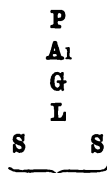


Fig. 1. Shows flower of *C. barbatum* described in the text. The column is shown as seen from the side.

Fig. 2. Diagram showing the arrangement of the parts in fig. 1.

petal P, and, opposite to it, a lip L. The column had one fertile median stamen, A₁, and in front of it one stigma, S^m, the other parts being absent. In Mr. Hansen's series of drawings I have seen illustrations of a similar malformation and dislocation in *C. Sedeni* ×, *C. barbatum*, *C. venustum*, and *C. Lawrenceanum*. The relative position of the parts in such flowers may be thus expressed:—

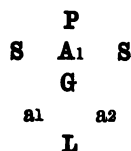


Diagrammatic illustration of figs. 1 & 2.

The lateral sepals are usually conjoined and, as it were, dragged out of place and made to assume a median position more or less opposite the upper median petal; but Mr. Hansen's drawings show various

(1878) June 18 and (1885) July 21; also Verhandl. d. Bot. Vereins d. Prov. Brandenburg (1882), xxiv. p. 111, and xxv. p. x, where other references to the literature of the subject are given. Dimerous flowers associated with the presence of one median fertile stamen, A₁, are frequently met with in this hybrid *Cypripedium*.

intermediate stages between perfect union and perfect dialysis of the sepals. Where the upper median sepal is present, it sometimes happens that the two lateral sepals are greatly reduced in size, so that various stages occur between the ordinary condition and one of dimery and decussation of parts. In all cases where the median stamen, A_1 , is fertile, the large shield-like staminode, \times , which forms so characteristic a feature in ordinary *Cypripedium* flowers, is absent. In one flower of *C. Lawrenceanum* in which the perianth was dimerous, the andrœcium was trimerous, the stamens present being one of the outer row, A_1 , and two of the inner row, a_1 , a_2 , thus :—



Diagrammatic illustration of arrangement in a monstrous flower of *C. Lawrenceanum*.

It will be observed that one stigma alone was developed in the median line, but whether that one represented G_1 or a combination of G_2 and G_3 , as under ordinary circumstances, I was not able to ascertain.

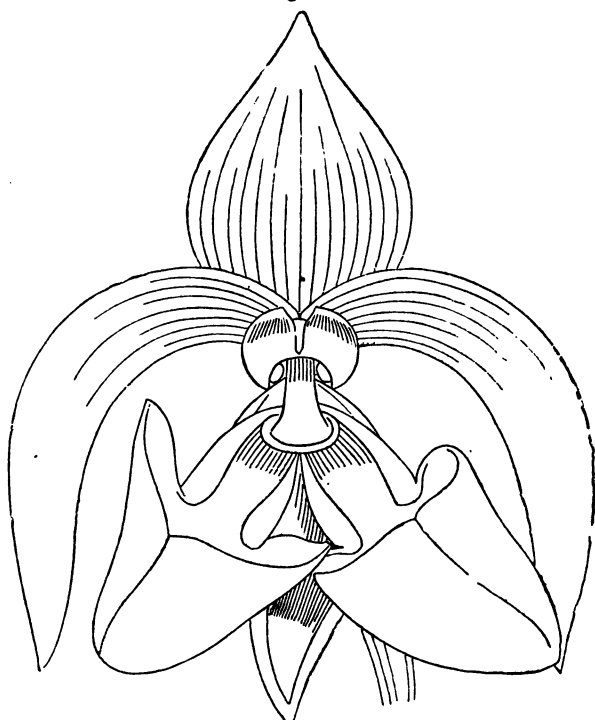
Monandrous and diandrous flowers have been already alluded to ; so that I may now pass on to flowers in which the number of stamens was greater.

PLEIOMERY.

II. *Increased Number of Parts*.—This is illustrated by the occasional presence of an increased number of lips. This augmentation may be due to an actual increase in the number of petals, to a division of one petal into two, or, more frequently, either to the development of the lateral petals in the form of lips, or to the appearance of one or more of the stamens in the guise of labella. An instance of increased number of petals in *Cypripedium superbiens* was lately communicated to me by Mr. James. In this flower the sepals, andrœcium, and the gynœcium were all normal ; but the corolla was represented by four petals, the two lower ones in the form of lips (see figs. 3, 4). Possibly these were not really two labella, but were constituted of one dividing into two at a very early stage ; but this could not be determined in the adult flower.

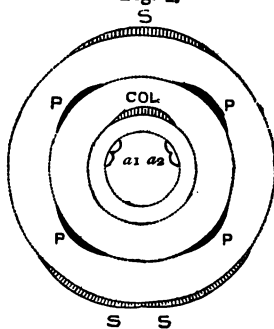
Plurality of the stamens occurs in different degrees. Hitherto I have not met with any absolute increase in number beyond the typical six ; but I have now met with instances of the presence in *Cypripedium* of from one to six stamens in different flowers, either in a fertile or in a petaloid condition, and upon some of these I shall now comment.

Fig. 3.

Two-lipped flower of *Cypripedium superbiens*.

Triandrous Flowers.—Magnus* describes a triandrous flower in *Cypripedium barbatum*; and I have seen a flower of the same species shown me by Mr. Lowne also with three stamens, viz. A_1 , a_1 , a_2 . In two flowers of *C. Lawrenceanum* (fig. 5), received from Mr. Stevens, the perianth was tetramerous and dicyclic, while the andrœcium was trimerous, the outer median stamen, A_1 , being fertile, and the two lateral stamens of the inner series, a_1 , a_2 , represented by shield-like staminodes, thus exactly reversing the

Fig. 4.

*Cypripedium superbiens*.

Plan of flower (fig. 3).—S, sepals; P, petals; COL, column or staminode; a_1 , a_2 , inner fertile stamens.

* Sitzungsber. d. Gesellsch. Nat. Freund. Berlin, June 18, 1878.

ordinary staminal arrangement in this genus. The stigma, G_1 , was superposed to the median fertile stamen. In a specimen of *C. Spicerianum* sent to me by Mr. Fraser, the three sepals were free, and the androecium was represented by the three stamens of the inner row a_1 , a_2 , a_3 all fertile. In *C. Sedeni* \times I have also seen all three stamens present in the case of flowers the subject of regular perioria to be hereafter mentioned.

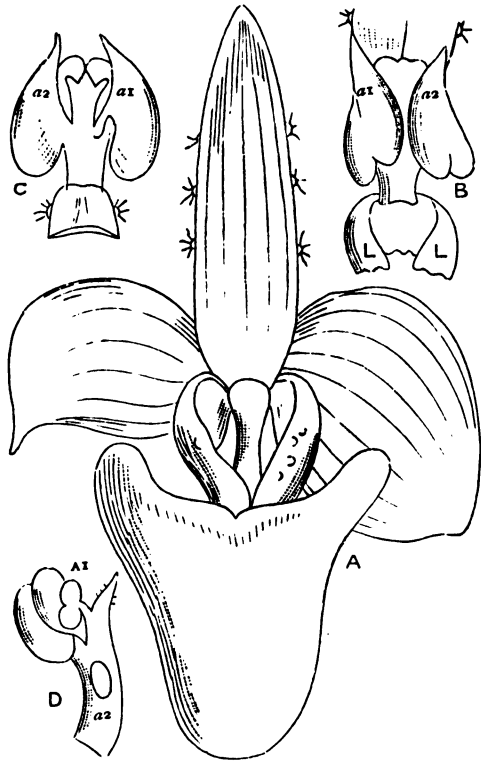
Tetrandrous

Flowers.—In *Uropedium* there are at least four stamens present, viz. A_1 , as a staminode, and a_1 , a_2 , a_3 fertile. The staminode in this case may possibly represent A_2 and A_3 as well as A_1 . Asa Gray describes* a tetrandrous flower of *Cypripedium candidum*; and I have lately examined a flower of *C. Lawrenceanum* in which there were four stamens present, viz. A_1 as a staminode, a_1 , a_2 fertile, and a_3 developed as a lip, which was, as it were, slipped within the cavity of the true lip, so that there were two lips one within the other (figs. 6 and 7).

In a *Cypripedium* sent me by Mr. Haywood there were also

* Seemann's Journ. of Botany, iv. (1866) p. 378.

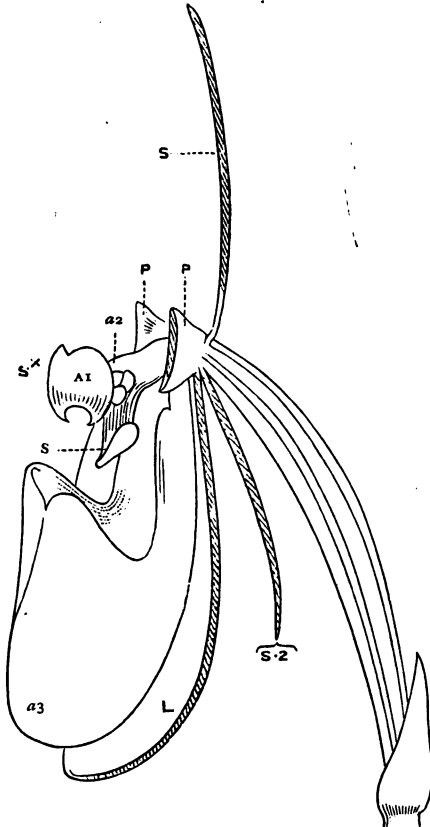
Fig. 5.



Flower of *Cypripedium Lawrenceanum*, with 4-parted perianth and three stamens, one outer, A_1 , fertile, two lateral, a_1 , a_2 , barren. A, flower; B, column, from the front; C, column, from the back; D, column, from the side, one of the staminodes, a_2 , removed.

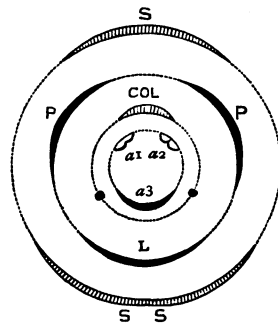
four stamens—*A*1, *a*1, and *a*2 developed as flat petals, while *a*3 was present in the form of a small lip. In this case not one of the stamens was fertile; but all were petalodic, as was also one of the styles *G*1, thus affording an instance of a double-flowered *Cypripedium** (fig. 8, p. 414).

Fig. 6.



Cypripedium Lawrenceanum.—Flower in section, with some of the parts removed to show one lip, *a*3, enclosed within the normal one *L*. *S*, sepals, the two lower ones conrescent; *P P*, petals cut across at their base; *A*1 staminode; *S*, stigma.

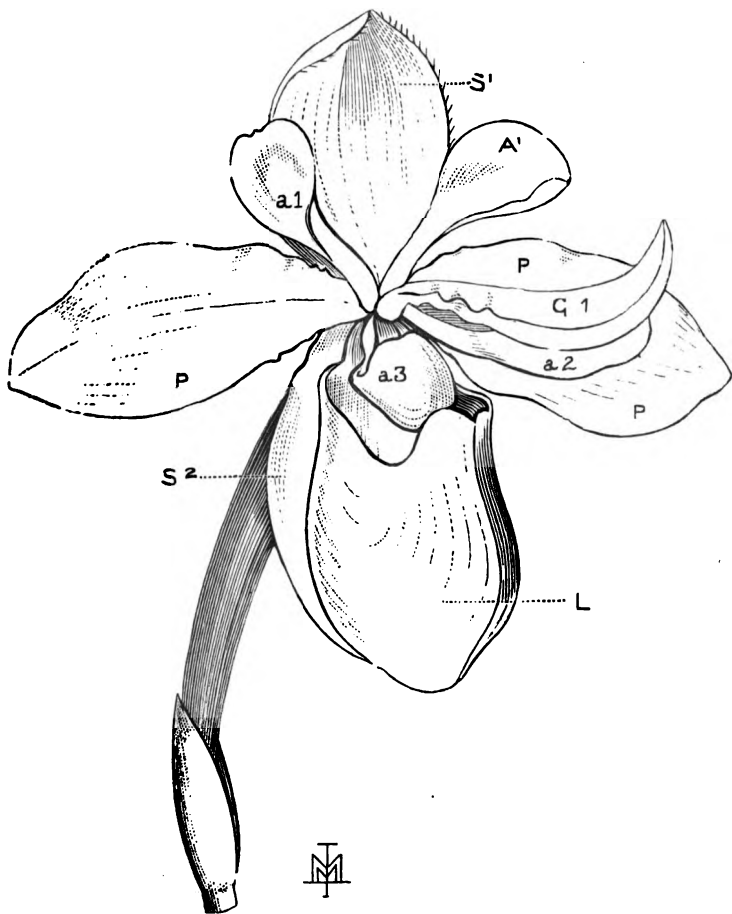
Fig. 7.



Cypripedium Lawrenceanum.
Plan of arrangement of parts.

* Masters in Gard. Chron. May 9, 1885, p. 597, fig. 112.

Fig. 8.

A double-flowered *Cypripedium*.

S₁, S₂, sepals; P, P, petals; L, lip; A₁, outer petal-like stamen; a₁, a₂, a₃, three inner stamens, of which two are petal-like and one lip-shaped; G₁, a petal-like style.

Hexandrous Flowers.—Last in the series may be mentioned a flower of *Cypripedium Sedeni* × in which all six stamens were present, two fertile, A₁ and a₃, opposite one another, while all the others were represented by saccate lips (irregular peloria).

Tendency to Increase the Inner Row of Stamens.

It is perhaps worthy of note that in the numerous cases I have examined, wherein the number of stamens in Orchids generally has been increased, the increase has been relatively more frequent in the inner staminal cycle than in the outer; thus, in my experience, it has been more common to find the inner series a_1 , a_2 , and even a_3 , developed either in a fertile or in a petalodic condition than it has been to meet with corresponding changes in the outer series A_1 , A_2 , A_3 . The frequent abortion of the outer row may be indeed induced by the necessities of space, or by the rhythmic alternation of activity and quiescence, which is so marked a feature in plant-life. In the nearly allied groups *Burmanniaceæ* and *Apostasiaceæ* the inner row of stamens is the one most usually developed, as it is also in *Restiaceæ* and *Xyridaceæ*; while in *Iridaceæ*, on the contrary, it is the outer episepalous row which is usually present, and the inner row is absent*.

PARTITION.

Under this heading may be included those cases in which an organ, primitively simple, becomes, in course of development, more or less divided by a so-called process of fission. They require to be carefully discriminated from instances of dialysis, or the separation of parts usually concrescent or inseparate. An illustration of this partition was afforded by a flower of *Cypripedium Spicerianum* forwarded by Mr. Hansen. In this flower the dorsal or median sepal, usually entire, had two distinct midribs and a shallow notch at the apex; the lower united sepals, the petals, the lip, the inner row of stamens a_1 , a_2 , and the stigma, G , were all of the usual form and appearance. The staminode, however, was divided to the base into two polygonal, shield-shaped lobes occupying a lateral, not a median, position. At first sight, therefore, it seemed as if the usual staminode representing A_1 were absent, while the other two of the outer row A_2 , A_3 were present in the form of petaloid shields. In fact, the appearance was exactly the same as in certain flowers mentioned in this communication in which the two side stamens of the inner row, a_1 , a_2 , were represented by shield-like staminodes.

* For a case in which the inner staminal series in *Iris* was developed, see Heinricher, Sitzungsab. der k. Akad. Wissensch. Wien, November 3, 1881, p. 509, separate paper, p. 51, tab. v.

That they did not, however, in this case, belong to the inner row was manifest, because the inner row was present in its normal state and position. Moreover, their insertion was distinctly external to that of the fertile stamens, while the back of the column presented a well-marked central ridge concealing a single central vascular bundle, which, near the apex, divided into three divisions—one central, minute, and two lateral, passing into the petal-like shields. The minute central portion evidently represents the central branch of the filament which in ordinary Orchids bears the anther, while the two lateral lobes are side-outgrowths from the same filament, thus resembling the trifid stamen of *Allium*, in which the central division bears the anther. Again, the indications of fission in the median sepal correspond to the similar division of the staminode superposed to it. Indications of this bipartition, or rather tripartition, of the posterior or median staminode are common in many species of *Cypripedium*, which present a central knob or boss and two lateral lobes.

On making sections through the peduncle, above the insertion of the bract, a ring of six vascular bundles was seen. At the base of the ovary the posterior bundle bifurcated; and this twin bundle was traced throughout the whole length of the prominent ridge forming the dorsal suture of G₁, and in to the median sepal S₁, where the bundles formed the double midrib. A similar section across the column at its base also showed six bundles, five single and one bifurcated; this bifurcated bundle passed into A₁, its two divisions passing into the shield-like divisions of the staminode. Thus the partition began at the base of the flower in the posterior median line, and continued in it all the way up; so that whereas, under ordinary circumstances, the arrangement in the median line would be—

in the particular flower now under consideration the arrangement was—

the gynæcium being only partially implicated, and the lip not at all.

S₁
A₁
G₁
L
S S
A A
G G
L

DISPLACEMENT.

III. *Change in Position of Parts.*—This has already been incidentally alluded to in connection with the reduced number of parts; but the importance of the subject necessitates some further mention. In the dimerous forms of *Cypripedium* the upper or median sepal is usually absent, the lateral ones are

present, either separate, when each occupies a truly lateral position, or united from concrescence, when the conjoined pair occupy a median, inferior, or anterior position. In these flowers the side petals are absent, the petalline whorl being represented by a single median petal opposite to the lip, as shown in Mr. Le Marchant Moore's monandrous *Cypripedium*, and in those figured in this communication, and as commonly happens when the flowers of Orchids are dimerous. Professor Charles Morren* describes and figures a flower of *Cypripedium insigne* in which, by torsion of the axis, the inner sepal had become lateral, and, by a further twist, one of the lower sepals was made to occupy the position of one of the lateral petals. Of the two side petals, one was completely absent, while the other, by a continuance of the twisting process, was placed in a median position opposite to the lip. All the stamens were absent except one of the inner row, apparently what we should now designate as *a1*. Morren cites this flower as an instance of what he terms "spiranthly." The flower may probably have been susceptible of other and simpler interpretations than that offered by the Belgian Professor; but it is unnecessary to enter into the question here, where the only object is to cite the flower as an instance of displacement of parts and of a monandrous condition.

In a flower of *C. Lawrenceanum* given me by Mr. O'Brien the flower had a peculiar oblique lopsided appearance by reason of the lateral petals being united with the upper sepal; and while the sepal was, as it were, dragged downwards, the petal was correspondingly raised; the consequence being that neither part occupied its natural relative position, 90° , but one was about midway between the two, *i. e.* 45° . The other lateral petal was normal in form and in position.

PELORIA.

IV. *Tendency towards Regularity of Form and Arrangement of Parts, or Peloria.*

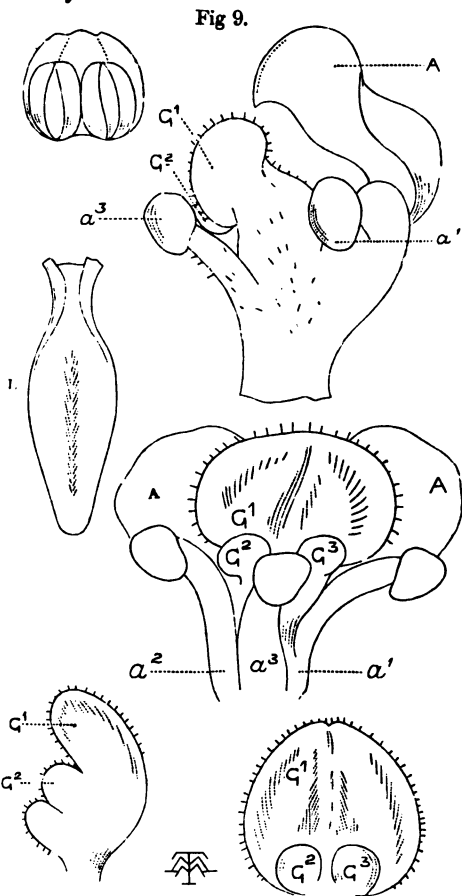
Peloria in *Cypripedium*, as in other plants, is either:—*α*, *Regular*, when the tendency to regularity is brought about by an increase in the number of regular portions, a tendency which seems to be a reversion to a simpler and probably primordial condition, as is the case perhaps in *Uropedium*; or, *β*, *Irregular*, when symmetry is restored by the development in an irregular

* Bull. Acad. Roy. Belgique, t. xviii. p. 196, tab.; *Lobelia* (1851), p. 55.

form of parts which are usually regular. Irregular Peloria, when not associated, as it sometimes is, with compensatory defect in other whorls, may be regarded as an instance of enhanced complexity and of potential progressive development. The opposite view, that the most highly complex is the form whence the less differentiated case of regular peloria is derived by a process of degeneration, finds, so far as I know, no warranty, either in organogeny or in anatomy.

Regular Peloria.—

Prof. Asa Gray, as before mentioned, has described a case of regular peloria in *Cypripedium candidum* associated with a reduced number of parts, forming thus a regular symmetrical and complete, but dimerous, Orchideous flower—the first verticil of stamens barren, the second antheriferous, and alternating with the carpels. Here we have, as Gray remarks, “clear, and perhaps the first, direct demonstration that the Orchideous type of flower has two staminal verticils, as Brown always insisted.”* Mr. Tautz has lately furnished me with a specimen of *Cypripedium* (or *Sele-*
nipedium) *Sedeni* ×,



Peloriate flower of *Selenipedium Sedeni*. Column, from beneath and from the side, anther, lip L, and stigmas G¹, G², G³. All magnified.

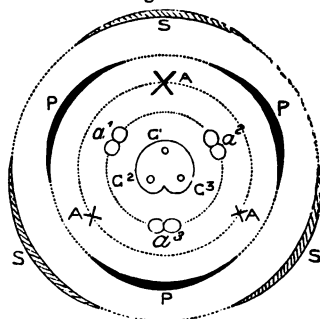
* Gray in Seemann's *Journal of Botany*, vol. iv. (1866) p. 378, reprinted from 'American Journal of Science,' xlii. July 1866. See also Magnus, 'Sitz-

in which there were three free sepals, two lateral petals, and one flat lip, like the other petals in shape but broader. The column had the usual staminode $A \times$ and two fertile stamens, a_1 and a_2 , with, in addition, a third stamen a_3 , projecting in front of the stigma. The stigma itself was three-lobed, the posterior lobe G_1 being of the usual large size, the two lateral lobes smaller (see figs. 9, 10). The formula for this very interesting flower is thus $3S \ 3P \times \ 3a \ 3G$.

The usual zygomorphic state was replaced by an actinomorphic condition, as is met with in some *Dendrobies*, *Paxtonia*, *Thelymitra*, *Phalænopsis*, *Telipogon*, &c. Endlicher's *Thelychiton* (Endl. Gen. 1616) may also be mentioned as a pelorioid form with a regular perianth and a cup-like andrœcium, one lobe of which bears an anther.

In a specimen of *C. caudatum* sent me by Mr. Bull (see Plate XX.) the three sepals were free, the lateral petals as usual prolonged into the long tails, which constitute so remarkable a feature of the species, while the median petal, instead of having the form of a long sac, something like the finger of a glove, was partially flattened out and partially contorted—presenting, in fact, an intermediate condition between that of the ordinary lip and that of one of the ordinary lateral petals. The median stamen of the outer row, A_1 , was present as a staminode; and the ear-like process on either side of it *possibly* represented the two lateral stamens of that series, A_2 , A_3 , though, from the analogy of other cases, I am more disposed to regard them as sterile branches of A_1 , and to consider that A_2 , A_3 were absent. The three inner stamens, a_1 , a_2 , a_3 , were all present and all fertile. The ovary was, as customary in this plant, 3-celled. So that there was in this flower a tendency towards regular peloria, and

Fig. 10.

Plan of peloriate flower of *Selenipedium* (see fig. 9).

ungeber. d. Botan. Vereins d. Prov. Brandenburg, xxi. January 31, June 27, and November 28 (1879); also his "Kurze Notiz über dimere Zygomorphie Orchideenblüthen und über ein monstroses *Cypripedium*," in the Abhandlung. d. Bot. Vereins Prov. Brandenburg, xxi. p. 97.

a reversion to the (assumed) primitive type, as manifested by the dialysis of the sepals (which, it may be incidentally mentioned, occurs normally in the Canadian *C. arietinum*), partial regularity of the lip, and the presence of the third or median stamen (as) of the inner row. The usual absence of this stamen seems to be correlated with the great development of the labellum. The stigma G_1 (marked S^m in the drawing) was superposed to as, either owing to the non-development of G_2 and G_3 , or, judging from other cases previously mentioned, it might have been really compounded of G_2 and G_3 . Unfortunately the arrangement of the vessels in the stigma of this flower was not examined.

In the flower in question the labellum was less highly organized than usual, and the stamen as consequently had more space wherein to develop, and thus the defect of the one was, to use Sir Thomas Browne's expression, "pierced out by the excess of the other." The close resemblance to *Uropedium** in Mr. Bull's flower was manifest in the dialysis of the sepals, the tendency in the lip to become regular, and in the presence of all the stamens of the inner cycle. In the Bulletin of the Amsterdam Botanical Congress, 1865, p. 62, Prof. Reichenbach describes a flower of *Selenipedium caudatum* in which the lip was undulated and twisted, bearing at its point a little thickening, as at the orifice of the bag-shaped lip. "If," says M. Reichenbach, "this flower had shown an anther in front of the labellum, it would have proved the identity of the two types (*Selenipedium* and *Uropedium*); but the flower, in spite of the petaloid nature of the labellum, had the column of *Selenipedium*, and on that account offers additional argument in favour of the distinctness of the two genera." In the specimen above described the third stamen was present in front of the lip, and so far it satisfied Prof. Reichenbach's postulate. For a figure of a very similar malformation in *S. caudatum* see also Reichenbach fil. in Nov. Acad. Nat. Cur. xxxv. (1870), n. 2, c. tab. In Reichenbach's plant the three sepals were not separate.

Irregular Peloria.—Cases of partial irregular peloria in *Cypripedium* are not very uncommon, as, for instance, flowers in which the lateral petals (or one of them) assume the saccate form of the lip. This may occur without any increase in the number of parts, or, on the contrary, some of the usually undeveloped

* *Uropedium*, see Brongniart, in Ann. Sc. Nat. sér. 3, xiii. p. 113; Reichenbach fil., 'Xenia' (1858), t. i. tab. 15; Bot. Zeit. 1876, p. 41.

stamens may be present in the form of lips, as in a flower of *C. Sedeni* ×, previously mentioned.

The change from the ordinary zygomorphic or irregular form to a state of actinomorphy or regularity is thus shown, not only in the equalized form and size of the parts of the flower, but also in their regularity of arrangement, either in a binary and decussate or in a ternary radiating manner. Whether the peloria be regular, or whether it be irregular, the result is thus seen to be the same—a zygomorphic flower becomes actinomorphic.

COMBINATION OF TENDENCIES.

The changes just referred to may occur separately, but it is more common to find them associated with others: thus an increased number of stamens is associated with regular peloria, and sometimes with independence of the sepals, as in Mr. Bull's specimen, or it may be that the increase in the number of stamens is connected with their development in the form of lips, as in irregular peloria. In irregular zygomorphic flowers, or in those which show a tendency to become so, it often happens that if one part, say the median sepal in *Cypripedium*, is larger than the lateral petals, the part opposite to it in the succeeding whorl is also larger than its fellows: thus in *Cypripedium* the large median or dorsal sepal is on one side of the flower, the largest petal (the lip) on the other; the large shield-like staminode is on one side, the large stigma on the other. This is of course a frequent tendency in flowers, as in *Eremophila*, where one large sepal is placed on the opposite side of the flower to the largest lobe of the corolla.

CHANGES RESULTING FROM HYBRIDIZATION.

The *Cypripedium Sedeni* ×, which presents so many monstrous conditions, is a hybrid raised in Messrs. Veitch's nursery, between *C. longifolium* and *C. Schlimii*, Rchb. f., in Gard. Chron. (1873), p. 1431. By its 3-celled ovary it falls into the section *Selenipedium*, which some prefer to consider a distinct genus, not only for structural, but also for geographical reasons, as it is the tropical American representative of the tropical Asiatic group. It is noteworthy that, according to Mr. Seden, the raiser, *Cypripedium Sedeni* × is produced whichever species be used as the seed-parent. Whether *C. longifolium* be fertilized by the pollen of *C. Schlimii*, or the reverse, the result is the same*. The

* Reichenbach, in Gard. Chron. l.c.; Veitch Orchid Conference Report, Journ. R. Hort. Soc. Lond. vii. (1886) p. 36.

petals of the hybrid are in form like those of *C. longifolium*, while their colour is that of *C. Schlumieri*.

The changes which occur in this and other hybrid plants and their derivatives may be ranged under three categories :—

1. Those in which there is an intermixture of parental characteristics, in varying degrees, but without any material change in the floral symmetry. The changes, in fact, occur in those characters which are more or less directly of an "adaptive" nature.

2. Those in which there is in the offspring more or less dissociation of the hybrid or mixed characters of the parents, so that the plant reverts more or less completely to one or other of its immediate parents, as pointed out by Naudin.

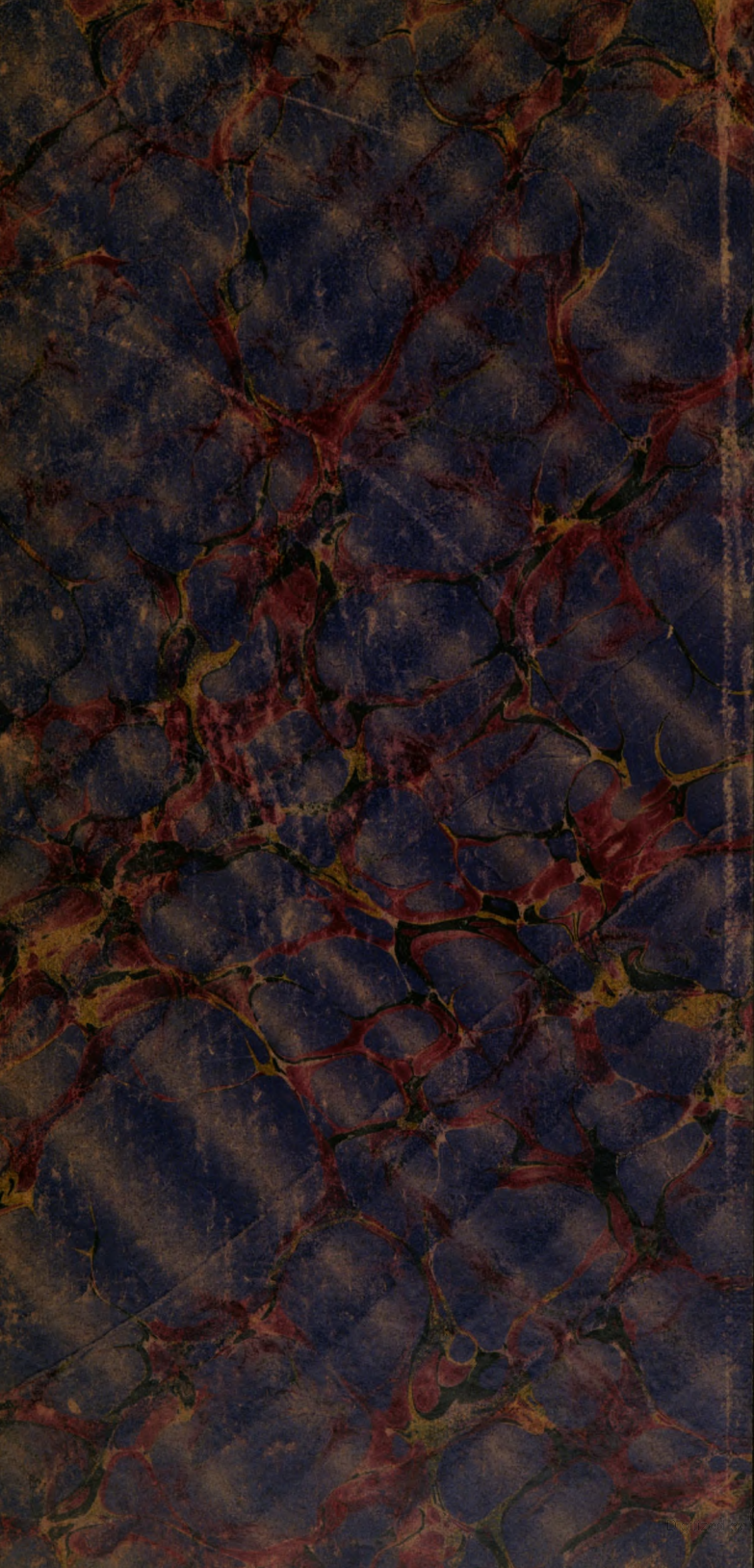
3. Those in which the change is decidedly teratological, and more or less affecting those "congenital" characters which constitute the symmetry of the flower. These may be: 1, reversions to an ancestral form, in which the structure was simpler, less differentiated, the parts possibly more numerous, and isolated rather than inseparable; or, 2, they may possibly be indications of the direction in which progressive modifications may take place in the future.

EXPLANATION OF PLATE XX.

Peloriote flower of *Selenipedium caudatum*, real size (see p. 419). A, section of ovary, magn. 4 diam.; B, side views of column, enlarged 3 times. A₁ A₂ A₃, staminode; A₂, A₃ are probably not separate stamens of the outer row as the lettering would indicate, but merely subdivisions of A₁; a₁, a₂, a₃, fertile stamens of the inner row; S^m, stigma. In the plan the signification of the letters is the same.







Arno